Prediction of actual primary production under nitrogen limitation

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Introduction

The value of natural rangeland as a feed source for ruminants is a function of both the quantity and the quality of forage present. These two characteristics alone may not suffice to give an adequate description of the feed source, because such factors as the distribution in space of the quantity (spatial heterogeneity), and quality (different organs) may exert a major influence on the feed value, but the former constitute the minimum required information. Extensive research in semi-arid regions, which are characterised by low and erratic rainfall, has shown that the two characteristics are not independent. There appears to be a much greater variability in the amount of water available for plant growth than in the amount of plant nutrients, both in time and in space. As a consequence, in years with favourable rainfall, production (quantity) will be determined by the availability of plant nutrients. Under such conditions, the concentration of the limiting element in the vegetation will reach some species-specific minimum value (quality). In unfavourable rainfall years, on the other hand, water will be the constraining factor and the element concentration in the tissue will remain well above the minimum value, thus providing higher-quality forage.

To characterise continuously the vegetation as a feed source it is necessary to keep track of the accumulation of both dry weight of the vegetation, which is a function of both moisture and nutrient availability, and the element content, which is a function of its availability in the soil. Models at various levels of detail describing the water balance in the soil have been developed, and, depending on the purpose of the model, provide adequate predictions of moisture available for the vegetation and its influence on production. Models of the nitrogen balance in the soil, its consequences for the availability of the element to the vegetation and the ensuing effect on growth and production are far less developed.

From: Modelling of extensive livestock production systems
Eds N. de Ridder et al. Proc. of ILCA-ARO-CABO workshop held at ARO, Bet Dagan, Israel, 1985.
International Livestock Centre for Africa, Addis Ababa, Ethiopia, 1986

In the first instance the aim of developing the present model was to predict the depth and duration of soil wetting, in an attempt to use those characteristics as an indicator for nutrient availability to the vegetation. Moreover, those characteristics may be of importance for the distribution of annuals and perennials in semi-arid regions. So far, these attempts have not been entirely successful, but efforts in this direction are being continued.

As a parallel effort, a simple nitrogen model was added in an attempt to predict primary production under variable conditions of moisture and nutrient availability.

Description of the model

Water balance

To describe the water balance, the total soil depth is subdivided into a number of compartments. In the present version, a total depth of 3 m is considered, consisting from the top downwards of 10 compartments of 0.05 m, five of 0.10 m and eight of 0.25 m. Both the total depth and the number of compartments can easily be changed.

A provision is built-in to take into account layered soils with a heterogeneous profile. In the present version restricted to five horizons. For each horizon, the depth below the soil surface has to be defined, as well as its properties with respect to the water-holding capacity, characterised here by the volumetric soil moisture content at field capacity, at wilting point and at air dryness, respectively. From a soil physical point of view, these characteristics are only loosely defined, because they are not inherent soil properties, but are co-determined by the boundary conditions (notably the depth of the groundwater table), and possibly plant properties (especially the lower value at which moisture is readily available to the plants). Such detail is, however, not considered in the present model.

Rainfall is introduced as a forcing function, derived from the nearest site where rainfall is gauged. If the site considered is far removed from the measurement site, a correction factor can be introduced, either based on intelligent guesswork, or on a more formalised procedure to generate rainfall data ('trend surface analysis').

Infiltration is derived from rainfall, taking into account interception by the vegetation, and the effect of soil surface properties, as expressed in run-off or run-on. Interception is difficult to quantify, but it is assumed that 1 mm of rainfall is intercepted by the vegetation irrespective of rain intensity or vegetation density. Run-off is calculated taking into account both average long-term run-off for a particular site, defined by a coefficient based on measurements, or on prior knowledge of the site and its soil properties, and the effect of rainfall intensity. The latter is described by an empirical relation that assumes a higher value for the run-off factor if rainfall intensity is higher. Implicitly the use of this function assumes that rainfall distribution over the day is always identical. The relation between rainfall intensity and run-off can be derived on the basis of a detailed, physically-based model of infiltration, as affected by soil hydraulic properties and surface characteristics (Rietveld, 1978). Application of such a model, however, requires detailed information on both soil properties and rainfall intensity. For most practical purposes, therefore, direct measurement of run-off seems more appropriate. In cases where such measurements are not available the run-off coefficient may be estimated on the basis of analogy, taking into account the effects of soil texture (Hoogmoed and Stroosnijder, 1984; Stroosnijder and Kone, 1982).

For the calculation of 'effective infiltration' an additional problem arises, related to the fact that the time resolution of the model is one day. If, in reality, rainfall occurs at the beginning of the day, i.e. between 0.00 and 9.00 hours, evaporation from the soil surface proceeds at the potential rate during that day and a substantial part of the water is lost. If, on the other hand, rainfall occurs after 18.00 hours, evaporation from the soil surface is negligible until the start of the following day, resulting in smaller losses (Stroosnijder and Kone, 1982). Because the timing of rainfall is not specified in the present model, it is assumed that it always takes place at the beginning of the day. As a consequence, the difference between potential soil evaporation and soil evaporation based on the actual top soil moisture content is subtracted before the water enters the soil profile. This formulation may lead to overestimation of soil evaporation, but at the present level of resolution any formulation will be arbitrary.

The moisture that enters the soil profile is distributed over the various soil compartments in such a way that they are filled to field capacity from the top downwards (van Keulen, 1975). This formulation thus assumes instantaneous equilibrium, i.e. within the time interval specified by the model. Subsequent compartments are filled up until total effective infiltration is dissipated or until the remainder has drained below the specified profile depth. Transport of moisture under the influence of gravity or under the influence of developing potential gradients is not taken into account. Of course, some redistribution of moisture will take place (Stroosnijder, 1976), and that can be described by defining field capacity at a somewhat lower value, resulting in slightly deeper infiltration.

The present model is intended for use in perma-dry conditions, where a water table is either absent or, if present, at such a great depth that it does not contribute to the moisture in the rooting zone. Hence, upward transport is not accounted for in the model.

Direct evaporation from the soil surface is an important source of non-productive water loss, especially under semi-arid conditions (Stroosnijder and Kone, 1982; van Keulen et al, 1981; van Keulen, 1975). For a proper description of the water balance, this process must therefore be described with some accuracy. A description based on physical processes is not possible in the framework of the present model, because the time constants of these processes are too small for time intervals of one day (van Keulen, 1975). Therefore, a parametrised description has been developed.

Potential evapotranspiration is introduced in the model as a forcing function. These values are calculated with a Penman-type equation, outside the model, but the calculation can also be incorporated in the model if the required meteorological data are available.

Potential evaporation from the soil is derived from potential evapotranspiration by subtracting potential transpiration by the vegetation. Thus, when the vegetation forms a closed surface, covering the soil completely, all available energy will be dissipated by transpiration and evaporation from the soil is negligible. As the next step, the influence of dessication of the top soil on evaporation from the soil is taken into account. This effect is derived from the assumption that, after an initial period, when soil evaporation is determined by energy availability (the 'constant-rate' stage), a 'falling-rate' stage follows, during which evaporation is determined by the rate at which moisture can be supplied to the soil surface. During the falling-rate stage a linear relation is assumed between cumulative soil evaporation and the square root of time (Stroosnijder and Kone, 1982; Ritchie, 1972). Hence, actual evaporation from the soil is derived from the slope of the relation between cumulative soil evaporation and square root time, and the time that has elapsed since the last effective rain shower, i.e. a shower that resulted in soil wetting.

As said before, transport between soil compartments under the influence of developing potential gradients is not explicitly incorporated in the model. However, evaporation from the soil surface results in redistribution of soil moisture by transport from deeper layers. In the present model that process is 'mimicked' following the procedure developed by van Keulen (1975), in which it is assumed that the total moisture withdrawal due to evaporation from the soil surface is distributed over the various soil compartments, following an exponential extinction function, and is moreover influenced by the actual moisture distribution in the soil profile. The extinction coefficient is a soil characteristic and can either be derived from experimental data, or from a detailed model of soil evaporation (van Keulen, 1975). The procedure has been described in detail by Stroosnijder (1981) and van Keulen (1975).

Potential transpiration is also derived from potential evapotranspiration, taking into account the effect of vegetation density and that of the nitrogen status of the vegetation. The influence of vegetation density is described under the assumption that potential transpiration by vegetation that does not cover the soil completely is proportional to its relative energy interception. The latter is calculated under the assumption of exponential extinction of irradiance (Goudriaan, 1977), with an extinction coefficient depending on vegetation type typically varying between 0.5 for erect gramineous vegetation and 0.7 for more planofile herbaceous vegetation. The degree of soil cover is mainly determined by the leaf area of the vegetation, but because that characteristic is not separately tracked in the present model, soil cover is related here to total above-ground biomass by a function that essentially describes the combined effect of specific leaf area and leaf-weight ratio (Watson, 1947).

The effect of the nitrogen status of the vegetation on potential transpiration is related to the mode of stomatal regulation. It appears that some species regulate stomatal opening in such a way that the CO_2 concentration inside the stomatal cavity is maintained at a near-constant value (Goudriaan and van Laar, 1978). Any condition that interferes with CO_2 assimilation then leads to partial stomatal closure in an attempt to reduce the influx of CO_2 into the stomatal cavity. One such condition is nitrogen shortage, the rate of CO_2 assimilation being proportional to the nitrogen concentration in the leaves over a wide range of concentrations (van Keulen and Seligman, 1985; Goudriaan and van Keulen, 1979; Wong, 1979). Hence, suboptimum nitrogen concentration in the leaf tissue results in lower CO_2 assimilation, followed by stomatal closure and consequently lower transpiration rates. In the model it is assumed that in the first period after germination sufficient nitrogen is available in the soil to maintain optimum nitrogen conditions in the vegetation, and that gradually the nitrogen store in the soil is depleted, leading to suboptimum levels. Potential transpiration is reduced in proportion to the ratio of actual growth rate and potential growth rate of the vegetation, taking into account the maintenance requirements.

Actual transpiration is derived from potential transpiration, taking into account the effect of root distribution and activity and soil moisture distribution. It is assumed that root density decreases linearly from the soil surface to the root tip. Root activity is calculated from root density, taking into account the moisture status of the various soil compartments. The latter is described by a schematic function that is zero when the soil moisture content is below wilting point, one when the soil moisture content is higher than 40% of the total plant-available moisture storage capacity (defined as the difference between wilting point and field capacity) and increases linearly in the intermediate range. Total root activity is then normalised in such a way that when the soil moisture status of the various compartments is favourable actual transpiration equals potential transpiration. In reality, some of the soil compartments may be too dry to allow unimpeded uptake of moisture by the roots. A reduction factor is introduced to account for the effect of suboptimum soil moisture conditions. This reduction factor is derived following a 'Veihmeyer-type' approach, i.e. soil moisture is readily available when soil moisture content exceeds 40% of the storage capacity, it is unavailable at wilting point, and availability decreases linearly in the intermediate range. For each soil compartment water uptake by roots is calculated as 'root activity factor' multiplied by the 'reduction factor' and potential transpiration. The sum of water uptake by the roots in the various compartments is equal to actual transpiration.

For each soil compartment the water balance is now completed, and the rate of change is calculated as: rate of inflow - rate of outflow - rate of soil evaporation - rate of root water uptake.

For special purposes, some auxilliary variables are calculated subsequently, such as the total amount of available moisture in the soil profile and the moisture status of the profile (a value being zero when no moisture is available in the root zone, or one otherwise). The number of days the soil moisture status is above wilting point is calculated for each compartment, which is used later to define the total wetting duration of the profile. That total wetting duration should be related to availability of nitrogen to the vegetation.

Growth of vegetation

The vegetation considered in the model is a mixture of annuals that starts from seed each year. For each site initial biomass after germination is defined, based on an estimate of the total seed stock in the soil and its germination characteristics.

Germination is assumed to take place in the upper 5 cm of the profile, whenever soil moisture in that soil layer is above wilting point. To calculate the moisture status of the soil layer for any particular day, infiltration on that day is also taken into account (rain is assumed to take place at the beginning of the day). If these conditions are fulfilled, the day is considered a germination day. Germination is considered complete when the number of germination days equals the total time required for germination, which is a species characteristic (Breman and Krul, 1982), in the present model an average value being used. For specific situations where the composition of the seed stock is known, a more accurate value can be introduced. If the top- soil dries out before germination is completed, the seedlings are considered to be dying and plant growth resumes only after a rainfall event rewets the top- soil.

At completion of germination, total above-ground biomass is initialised with the predefined initial value. The increase in biomass is defined by a relative growth rate in the early stages of plant growth. In the present version a value of 0.15/d is defined, being typical for a mixture of annuals in Sahelian conditions (Penning de Vries, 1982). These growth rates can be realised, because in the initial stages sufficient plant nutrients are available in the soil to ensure optimum concentrations in the vegetation (Penning de Vries and van Keulen, 1982). When the growth rate calculated on the basis of the constant relative growth rate exceeds a predefined maximum value, that value is substituted.

For both situations, the growth rate is corrected for the ratio of actual and potential transpiration, under the assumption that CO_2 assimilation is reduced in proportion to the reduction in transpiration. That assumption is based on extensive experimental evidence and theoretical treatment of the processes (cf Tanner and Sinclair, 1983; de Wit, 1958).

If the soil dries out, transpiration gradually declines until the whole root zone is at (or below) wilting point, at which point stomata are fully closed and CO_2 assimilation ceases. When such conditions last for some time the vegetation will react with processes that decrease transpirational demand, such as leaf rolling and leaf shedding. In the present model these phenomena are not taken into account in a dynamic way. The number of days on which there is no transpiration is tracked in the model and if it exceeds a certain predefined value, characterising the buffering capacity of the vegetation, the vegetation is assumed to die completely in one day. If a rainfall event occurs before that day is reached, the accumulated stress days are zeroed and accumulation starts again after that moisture has been depleted.

The total number of growing days of the vegetation is tracked by integrating each day that actual transpiration assumes a non-zero value.

Dry-matter accumulation in the roots is not considered in the model, because the growth rate is defined on an above-ground basis only. Rooting depth is, however, considered: the rooting depth at emergence is assumed to be 0.075 m, and under optimum conditions the rate of root extension is 0.04 m/d. Root extension proceeds at that rate until the root tip reaches a soil compartment that is at or below wilting point, after which root extension ceases. Root extension also ceases when a predefined maximum rooting depth has been reached.

The nitrogen balance

The major characteristic of the nitrogen balance, as described in the present model, is that it is highly empirical, which means that it can only be used with extreme caution outside the range of conditions for which the model has been calibrated. In this first approximation several assumptions have been introduced that simplify reality substantially and it may well be necessary to replace some of these during further development of the model.

The mineral nitrogen in the soil is assumed to be in nitrate form, even though in reality some may be present in the form of ammonium (Krul et al, 1982).

At the start of the simulation, an initial amount of mineral nitrogen is assumed to be present in the soil, originating largely from the previous year's root material that has partly decayed. The amount present is therefore proportional to the amount of roots present, for which a typical value for annual vegetation in the Sahel has been chosen (Penning de Vries and van Keulen, 1982).

Mineral nitrogen in a soil compartment can increase by decomposition of organic material, it being assumed that during the growing season the microbial population is more or less in equilibrium, so that all nitrogen in the decomposing material contributes to the mineral nitrogen store. The rate of decomposition is derived from the total amount of organic material present, assuming a constant relative decomposition rate, and taking into account the effect of soil moisture status on microbial activity. In the present model, essentially the relation as given by Beek and Frissel (1973) is used, although conflicting evidence is available in the literature (Stanford and Epstein, 1974; Robinson, 1957).

In the first soil compartment two more processes contribute to mineral nitrogen. Firstly, the influx by rain, which also represents fixation by blue-green algae and free-living bacteria. The concentration of N in rainwater is assumed to be 0.0125 kg/mm. Secondly, decomposition of litter on the soil surface, which consists of plant remnants from the previous season, also provides inorganic nitrogen to the top soil compartment. The rate of decomposition of litter is described in a similar way as for the organic matter in the soil, i.e. a constant relative decomposition rate, corrected for the moisture content in the top soil compartment.

It is assumed that the contribution of stable organic material to the supply of mineral nitrogen is negligible.

A major problem in the description of the processes of the nitrogen balance treated so far is that estimates have to be made of the initial size of the various components. In the calibration runs most of the values were derived from experimental data collected in the Sahelian zone (Penning de Vries and Djitèye, 1982).

Mineral nitrogen will move with water flow. Hence, during a rainfall event, leaching of nitrogen may take place. The rate of outflow of nitrogen from any compartment is calculated as the rate of water flow from that compartment multiplied by the average concentration of nitrogen in the 'outflow' and the 'inflow' compartment. Finally, that value is multiplied by a 'leaching efficiency' (van Veen et al, 1981).

Uptake of nitrogen by the vegetation is assumed to take place only passively, i.e. with the transpiration stream. The rate of uptake from each compartment is thus obtained as root water uptake multiplied by the concentration of N in that compartment, multiplied by a nitrogen uptake efficiency. Total uptake of nitrogen by the vegetation is the sum of uptake from the various compartments in the root zone. This formulation may be an oversimplification, because in reality it seems that if the demand for nitrogen of the growing vegetation is higher than can be supplied by passive uptake, additional uptake can take place by diffusion of nitrogen to the root surface (van Keulen et al, 1975).

For each soil compartment, the nitrogen balance is now completed by formulating the rate of change as: rate of mineralisation plus rate of inflow from the overlying compartment minus rate of outflow to the underlying compartment minus rate of root nitrogen uptake.

Some model specifications

A complete listing of the model, formulated in the simulation language CSMP is given in Appendix 1, while a glossary is provided in Appendix 2.

As explained earlier, the time interval of integration is one day, and integration is performed according to the simple rectilinear integration method.

Results and discussion

It should be stressed that the results presented are of a preliminary nature, because the model is still under development and further adaptations and changes are certainly necessary.

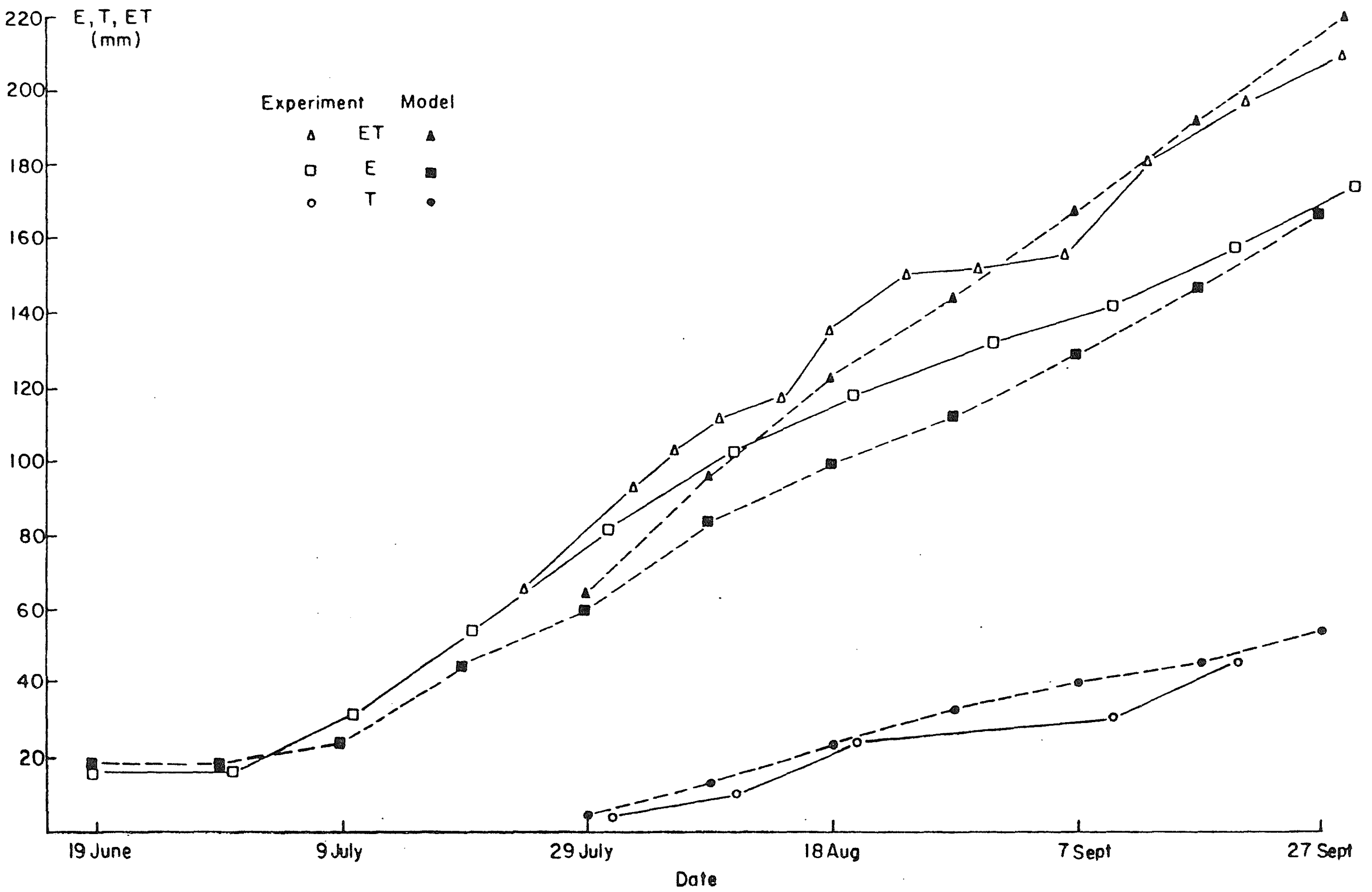
Calibration runs were carried out with data from an experiment carried out in Niono, Mali (5^{o} 45'W, 14^{o} 30'N), in 1978 on a sandy soil (Stroosnijder and Kone, 1982).

The measured and calculated terms of the water balance are given in Figure 1. In the experiment total evapotranspiration was determined by measurement of total soil moisture by neutron moderation, taking into account infiltration as measured at the site. Evaporation from the soil was determined separately and the difference between the two terms was calculated as crop transpiration. This results in the observation that cumulative transpiration sometimes declines, a situation that in reality will not have occurred.

Measured and simulated values are of the same order of magnitude, although individual values sometimes deviate up to 15%. However, taking into account the simple description of the water balance and the fact that the soil at the experimental site is rather heterogeneous, whence it is difficult to define soil physical parameters unequivocally, the results are satisfactory.

The calculated biomass at day 268 (25 September) was 1860 kg/ha, which is substantially higher than the 1400 kg/ha measured in the experiment. However, at that particular site the vegetation consisted predominantly of Zornia glochidiata, a leguminious species with a relatively short growth cycle and hence a low total dry-matter yield. The average yield on the sandy soil of the ranch was substantially higher that year and may have approached the calculated value. In the Zornia plot growth of the vegetation ceased before day 268, not because of moisture shortage (even after that day there was sufficient moisture in the soil to sustain plant growth) but due to photoperiodic effects. It has been observed in the Sahelian region that most of the plant species are very photoperiod-sensitive. In the model this effect is not incroporated, so that only moisture shortage causes cessation of growth. Evidently, this omission affects the degree of realism of the model, and, if possible, some sort of quantitative description of the effect of photoperiodism on phenological development of the vegetation should be included.

Figure I. Measured and calculated values of evaporation (E), transpiration (T) and evapotranspiration (ET), Niono, Mali, 1978



From a comparison of the measured and simulated soil moisture profiles on three dates during the growing season (Figure 2), it appears that the model predictions are not very accurate. The depth of wetting is much deeper in reality than calculated by the model. However, simulated ET values are similar to the measured values (Figure 1), so the main difference is in the distribution of soil moisture. The reason(s) for these discrepancies are not clear: it could be speculated that redistribution of moisture takes place under the influence of gravity, a process not accounted for in the model. Such an effect could be mimicked in the model by assuming a somewhat lower value for field capacity, thus inducing deeper infiltration. Experimentation with the model has shown, however, that to achieve the measured depth of wetting, unrealistically low values would have to be introduced. It seems, therefore, that at this stage the various terms of the water balance and their description in the model need to be reconsidered. These results are somewhat disappointing, because one of the aims of the model is to predict total nutrient uptake by the vegetation as a function of the depth and duration of soil wetting, based on the assumption that nutrient supply from the soil is mainly determined by that characteristic (cf Harpaz, 1975).

In Figure 3 measured and simulated uptake of nitrogen are compared using data from a transect in the Sahel studied for four consecutive seasons (Breman and Krul, 1982). There is considerable scatter in the data, but this may be partly attributed to the fact that no attempt was made to include site- or year-specific information for the description of the nitrogen balance in the model.

The relationship with integrated soil wetting is illustrated in Figure 4, using the same data. Despite the fact that the moisture distribution in the calibration runs was not very satisfactory, it seems that a relationship exists between the calculated product of depth and duration of soil wetting and total nitrogen uptake as measured in the field. Longer wetting generally leads to higher nitrogen availability, up to a value of about 1500 layer.d, after which levelling off occurs. These results indicate that the length of the period during which conditions are favourable for microbial activity, and hence for decomposition of organic material, is a major determinant of the soil nitrogen supply.

Figure 2. Measured and simulated soil moisture profiles on three dates during the growing season, Niono, Mali, 1978

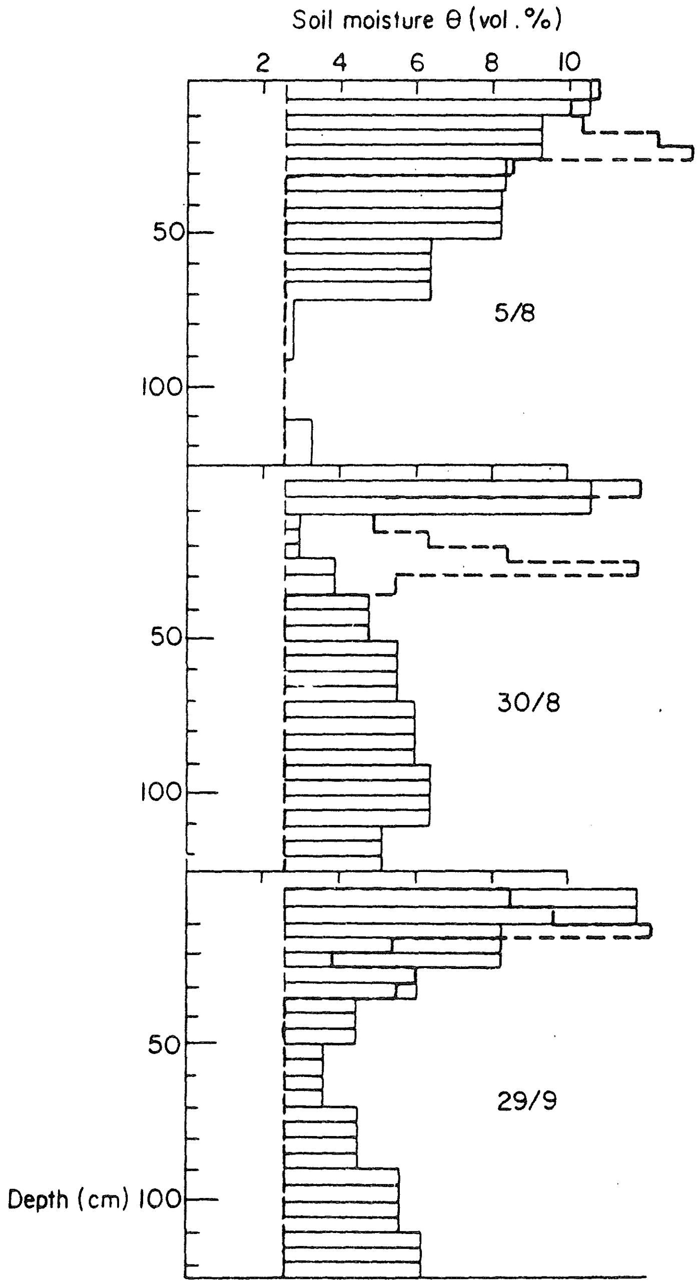


Figure 3. Relationship between measured and simulated uptake of nitrogen of vegetation, with and without a legume component, from a transect in the Sahel, 1976-79

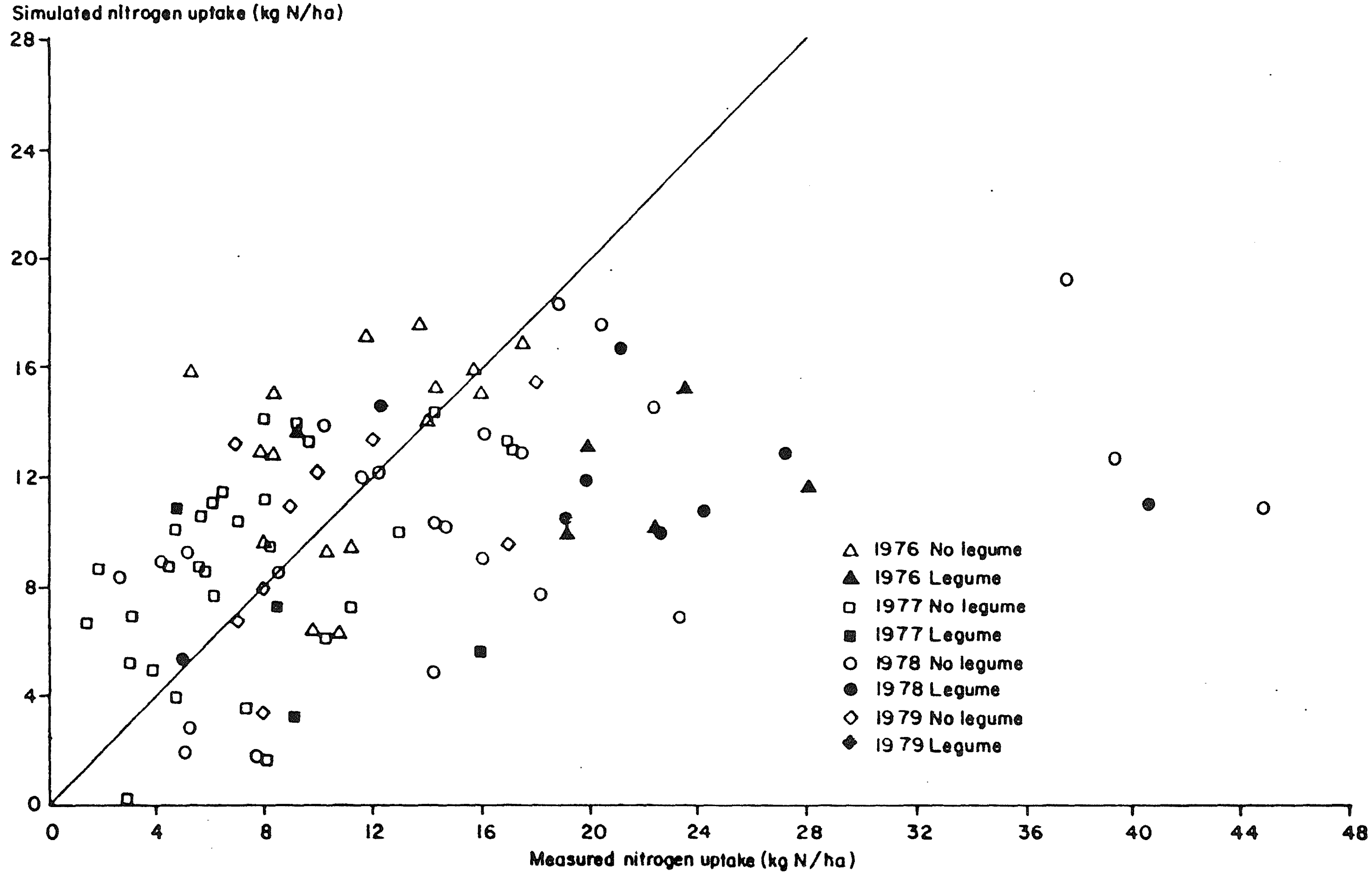
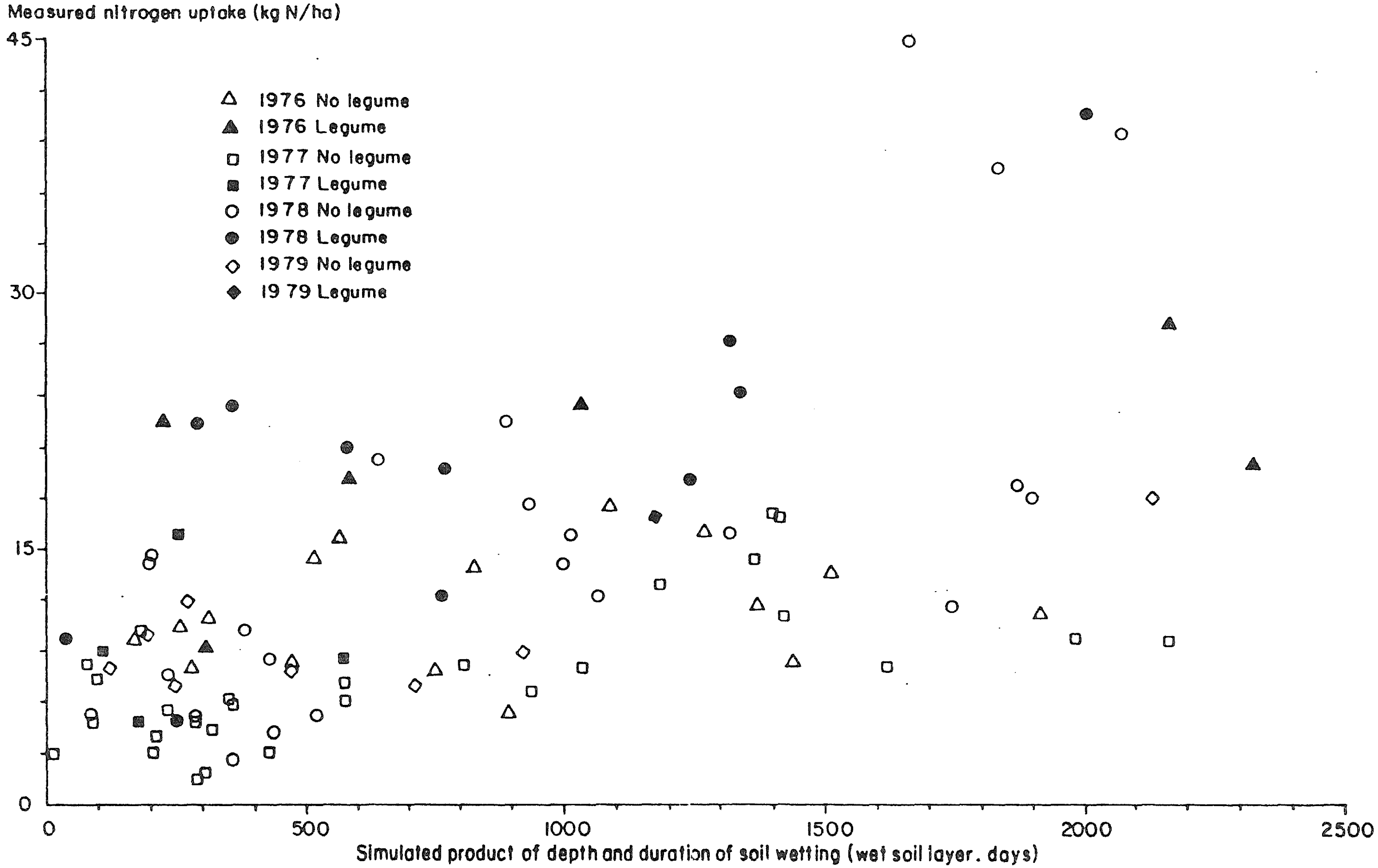


Figure 4. Relationship between the simulated product of depth and duration of soil wetting (wet soil layer. days) and measured nitrogen uptake (kg N/ha) of vegetation, with and without a legume component, from a transect in the Sahel, 1976-79



The scatter of the data is still rather large for which there are a number of possible reasons:

1. In the present description no distinction is made between soil wetting in the surface horizons, where most of the organic material is concentrated, and in deeper layers. Improvements in the relation could possibly be expected if the wetting depth and duration were weighted for organic matter content of the soil.
2. The field data, covering many different sites and a number of years, cover a large variety of vegetation types. The composition of the vegetation differs considerably from year to year and from site to site. This phenomenon has consequences for the nitrogen economy as well, because different species may mature at different times. Therefore, it could be that, at harvest time at the end of the rainy season, some of the nitrogen that was taken up by the vegetation was lost already by seed shedding, especially because those organs act as a strong sink for nutrients at the end of the plant's life cycle (de Ridder et al, 1981). One of the factors that causes discrepancies is the proportion of legumes in the final biomass. Most data points for which more than 20% of the final biomass consisted of legumes are at the upper side of the graph, indicating the contribution of nitrogen fixed from the atmosphere.
3. In the present formulation it is assumed that practically all the nitrogen available to the vegetation in the current season originates from plant remnants from the previous season. Thus, more nitrogen would be available after a relatively favourable season with a large biomass than after a relatively unfavourable season, while in a favourable season following a drought year there could be some contribution from residual nitrogen that was not taken up in the water-limited year. None of these differentiations have been taken into account in the model.

Concluding remarks

The model as presented in this paper can be considered partly as a summary model (Penning de Vries, 1982), comprising simple descriptions of processes that are relatively well understood. Partly, however, the model is highly empirical and therefore speculative, especially for the soil- and vegetation-nitrogen balances.

In some respects, particularly (evapo)transpiration and dry-matter production, the performance of the model is reasonable; in other aspects, for instance moisture distribution, its performance is rather weak. More work is needed on these.

Another aspect that needs further study is the relationship between the nitrogen status of the vegetation and its growth and production. In the present formulation these two characteristics are completely independent, the growth rate being derived from experimental data. A more fundamental approach, whereby the processes of assimilation and respiration as influenced by the nitrogen status of the vegetation are considered, could be an attractive alternative (cf van Keulen and Seligman, 1985).

All-in-all it may be concluded that the present model is a useful first approximation for the description and understanding of natural vegetation in semi-arid regions, but that for wider application further development is necessary.

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Appendix 1   Model listing.

```
      TITLE SAHEL MODEL
      SYSTEM NPOINT = 2000.
      SYSTEM BCD
      INITIAL
      NOSORT
      STORAGE AIRDR(25),  AIRDRY(5),  BOUND(5),   DPTH(25), ...
              DPTHC(25),  EVAPR(25),  F(25),      FLDCAP(5), ...
              FLDCP(25),  MF(25),     NCONC(25),  NLEACH(25), ...
              NUPTAK(25), RDENF(25),  RDSUBS(25), RNMIN(25), ...
              RRDENF(25), STORC(25),  TCK(25),    TRAN(25), ...
              VAR(25),    WIN(25),    WLTPNT(5),  WLTPT(25)
      FIXED I,N,K
      PARAM N = 23
      TABLE TCK(1-23) = 10*50.,5*100.,8*250.
      TDEPTH  = 0.
      DEPTH(1) = 0.
      DO 10 I  = 1,N
      DPTH(I+1)  = DPTH(I)+TCK(I)
      TDEPTH     = TDEPTH +TCK(I)
      DPTHC(I)   = DPTH(I)+0.5*TCK(I)
 10   CONTINUE
      K        = 1
      DO 30 I = 1,N
      WLTPT(I)  = WLTPNT(K)
      FLDCP(I)  = FLDCAP(K)
      AIRDR(I)  = AIRDRY(K)
      STORC(I)  = FLDCP(I)-WLTPT(I)
      IF(DPTH(I+1).LT.BOUND(K)) GOTO 20
      K          = K+1
 20   CONTINUE
 30   CONTINUE
      DO 40 I = 1,N
      WI(I)  = TCK(I)*AIRDR(I)
 40   CONTINUE
```

```
      INCON CROPSI = -1.
      RTDI  = RTDG
      TABLE SUBSTI(1-23) = 2*325.,2*100.,2*65.,2*35.,2*10.,3*7.,...
                           2*5.,4*3.,4*0.
      DO 50 I = 1,N
      INI(I) = IFRMN*SUBSTI(I)
50    CONTINUE
      DYNAMIC
      NOSORT
      DAY     =   STDAY+TIME
      RAIN    =   ISOHC*AFGEN(RAINTB,DAY)
      INTC    =   INSW(1.0-RAIN,1.0,RAIN)
      RNOFF   =   RNOFFC*AFGEN(ROFINT,RAIN)*RAIN
      INFR    =   RAIN-RNOFF-INTC
      PETNR   =   AFGEN(PETNRT,DAY)
      PETR    =   AFGEN(PETRT,DAY)
      RNPAR   =   INSW(RAIN-0.001,-1.,1.)
      EVAPTR  =   INSW(RNPAR,PETNR,PETR)
      SCOV    =   1.0-EXP(-0.5*BIOM/AFGEN(SSWTB,BIOM))
      PDGRT   =   LIMIT(0.,1.,BIOM/2500.)*PDGRTM
      NFACT   =   AMIN1(1.0,(1.5*DGRATE+.015*BIOM)/...
                  (1.5*PDGRT+.015*
                  (BIOM+NOT(BIOM))))
      TRANP   =   SCOV*INSW(CROPST,0.,EVAPTR)*NFACT
      EVAPP   =   AMAX1(0.,EVAPTR-TRANP)
      DSLER   =   INTGRL(90.001,1.-INSW(RAIN-0.001,0.,...
                  INSW(EVAPP-INFR,DESLER-0.001,0.)))
      AEVAP   =   AMIN1(EVAPP,EVAPC*(SQRT(DSLER)-SQRT(DSLER-1)))
      SUMRRD  =   0.
      DO 60 I = 1,N
      EFFAC    = AFGEN(EFFACT,AMIN1(1.0,(W(I)/TCK(I)-WLTPT(I))/...
                 STORC(I)))
      RRDENF(I) = TCK(I)*EFFAC*AMAX1(0.,(RTD-DPTHC(I))/...
                  (RTD+NOT(RTD)))
      SUMRRD   =  SUMRRD+RRDENF(I)
```

```
   60 CONTINUE
      DO 70 I = 1,N
      RDENF(I) = RRDENF(I)/(SUMRRD+NOT(SUMRRD))
      TRAN(I)  = 0.
      EVAPR(I) = 0.
   70 CONTINUE
      STRAN = 0.
      DO 80 I = 1,N
      REDF = LIMIT(0.,1.,(W(I)/TCK(I)-WLTPT(I))/(LMF*STORC(I)))
      TRAN(I) = RDENF(I)*REDF*TRANP
      STRAN =  STRAN+TRAN(I)
      IF(DPTH(I+1).GT.RTD) GOTO 90
   80 CONTINUE
   90 CONTINUE
      SUMT   = 0.
      DO 100 I = 1,N
      VAR(I) = AMAX1(W(I)/TCK(I)-AIRDR(I),0.)*EXP(-0.001*PROP...
                *DPTHC(I))
      SUMT   = SUMT+VAR(I)*TCK(I)
  100 CONTINUE
      SEVAP  = 0.
      DO 110 I = 1,N
      F(I)    =  TCK(I)*VAR(I)/(SUMT+NOT(SUMT))
      EVAPR(I) = AMIN1(W(I)-TCK(I)*AIRDR(I),F(I)*AEVAP)
      SEVAP  =  SEVAP+EVAPR(I)
  110 CONTINUE
      EVAPPR = AMAX1(0.,EVAPTR-INTC-STRAN)
      WIN(1) = AMAX1(0.,INFR-EVAPPR)
      SEVAP  = INSW(WIN(1)-0.001,SEVAP,EVAPPR)+INTC
      DO 120 I = 2,N+1
      WIN(I) = AMAX1(0.,WIN(I-1)-(FLDCP(I-1)*TCK(I-1)-...
                (W(I-1)-INSW(WIN(1)-0.001,EVAPR(I-1),0.)-...
                TRAN(I-1)))/DELT)
  120 CONTINUE
      DO 130 I = 1,N
```

```
      RCW(I) = WIN(I)-WIN(I+1)-INSW(WIN(1)-0.001,...
                EVAPR(I),0.)-TRAN(I)
130   CONTINUE
      W       = INTGRL(WI,RCW,23)
      WGER    = 0.
      DO 140 I = 1, N
      IF(DPTH(I+1).GT.GDPTH) GOTO 150
      WGER     = WGER+W(I)
140   CONTINUE
150   CONTINUE
      WGER     = WGER+INFR
      WTOTR    = 0.
      MSSTAT   = 0.
      DO 160  I = 1,N
      WTOTR    = WTOTR+W(I)*LIMIT(0., TCK(I),RTD-DPTH(I))/TCK(I)
      MSSTAT   = MSSTAT+INSW(W(I)-WLTPT(I)*TCK(I)-.001,0.,1.)*...
                 LIMIT(0.,TCK(I),RTD-DPTH(I))/TCK(I)
      IF(DPTH(I+1).GE.RTD) GOTO 170
160   CONTINUE
170   CONTINUE
      GERD     = FCNSW(WGER-GDPTH*WLTPT(1),1.,1.,0.)
      MSFG     = INSW(CROPST, INSW(WGER-GDPTH*WLTPT(1),0.,1.),0.)
      EMPTR    = AND(GERD,MSSTG)*MSSTG/DELT
      PUSHE    = AND(-CROPST,MSSTG-GERMT)
      MSSTG    = INTGRL(0.,MSFG*(1.-PUSHE)-PUSHE*MSSTG/DELT-EMPTR*...
                 (1.-PUSHE))
      KILD     = FCNSW(STRAN,0.,0.,1.)
      PUSHD    = AND (CROPST,MSSTD-DEADT)
      MSFD     = INSW(-STRAN,0.,1.)*INSW(CROPST,0.,1.)*(1.-PUSHD)
      EMPTRR   = AND(KILD,MSSTD)*MSSTD/DELT
      MSSTD    = INTGRL(0.,MSFD-PUSHD/DELT*MSSTD-EMPTRR*(1.-PUSHD))
      SWPDS    = 0.
      DO 180 I= 1,N
      SWPDS    = SWPDS+AND(RTD-DPTH(I)+0.001,DPTH(I+1)-RTD)*...
                 INSW(W(I)-WLTPT(I)*TCK(I),0.,1.)
```

```
180   CONTINUE
      GRTD    = INSW(CROPST,0.,INSW(MXRTD-RTD,0.,OGRTD*SWPDS))*...
                (1.-PUSHD)
      RTD     = INTGRL(0.,RTDI*PUSHE/DELT+GRTD-PUSHD/DELT*RTD)
      GRRATE  = AMIN1(RGR*BIOM,DGRATE)*STRAN/(TRANP+NOT(TRANP))
      RGROW   = GRRATE/(BIOM+NOT(BIOM))
      TRR     = STRAN/(TRANP+NOT(TRANP))
      BIOM    = INTGRL (0.,IBIOM*PUSHE/DELT+GRRATE*(1.-PUSHD)-...
                PUSHD*BIOM)
      TDBIOM  = INTGRL(0.,PUSHD*BIOM)
      CROPST  = INTGRL(CROPSI,PUSHE*2.-PUSHD*2.)
      GROWD   = INSW(CROPST,0.,1.)*INSW(MSSTAT-.001,0.,1.)
      TGROWD  = INTGRL(0.,GROWD)
      TOTNUP  = 0.
      DO 190 I= 1,N
      NCONC(I)= NI(I)/W(I)
      NUPTAK(I) = AMIN1(NI(I),NUE*NCONC(I)*TRAN(I))
      TOTNUP  = TOTNUP+NUPTAK(I)
190   CONTINUE
      DO 200 I= 1,N
      NLEACH(I) = AMIN1(NI(I)-NUPTAK(I),LE*WIN(I+1)*(NCONC(I)+...
                  NCONC(I+1))/2.)
      MF(I)   = AFGEN(MFT,AMAX1(O.,(W(I)/TCK(I)-WLTPT(I)))/...
                STORC(I))
      RDSUBS(I) = RDR*MF(I)*SUBSTR(I)
      RCSUBS(I) = -RDSUBS(I)
200   CONTINUE
      RCLIT   = RDLIT*MF(1)*LITTER
      RNMLIT  = FRNLIT*RCLIT
      RNMIN(1)= FRNR*RDSUBS(1)
      RCN(1)  = NCR*INFR+RNMLIT+RNMIN(1)-NLEACH(1)-...
                NUPTAK(1)
      TRNMIN  = RNMIN(1)
      DO 210 I= 2,N
      RNMIN(I) = FRNR*RDSUBS(I)
```

```
      TRNMIN  = TRNMIN+RNMIN(I)
      RCN(I)  = RNMIN(I)+NLEACH(I-1)-NLEACH(I)-NUPTAK(I)
210   CONTINUE
      TMINR   = INTGRL(0.,TRNMIN)
      TMINL   = INTGRL(0.,RNMLIT)
      TMINRL  = INTGRL(0.,TRNMIN+RNMLIT)
      LITTER  = INTGRL(ILIT,-RCLIT)
      SUBSTR  = INTGRL(SUBSTI,RCSUBS,23)
      NI      = INTGRL(INI,RCN,23)
      NDBIOM  = INTGRL(0.,PUSHD*TNITUP)
      TNITUP  = INTGRL(0.,IFRNB*IBIOM*PUSHE/DELT+TOTNUP*(1.-PUSHD)-...
                PUSHD*TNITUP)
      NCBIOM  = TNITUP/(BIOM+NOT(BIOM))
      TSUBST  = 0.
      TOTNI   = 0.
      DO 220 I= 1,N
      TSUBST  = TSUBST+SUBSTR(I)
      TOTNI   = TOTNI+NI(I)
      RAVW(I) = FCNSW(W(I)-WLTPT(I)*TCK(I),0.,0.,1./DELT)
      RAVW1(I) = RAVW(I)*MF(I)
220   CONTINUE
      AVW     = INTGRL(IAVW,RAVW,23)
      AVW1    = INTGRL(IAVW,RAVW1,23)
      TAVW    = 0.
      TAVW1   = 0.
      DO 230 I= 1,N
      TAVW    = TAVW+AVW(I)
      TAVW1   = TAVW1+AVW1(I)
230   CONTINUE
      GERWAV  = INTGRL(0.,PUSHE)
      GDAY    = INTGRL(0.,PUSHE*TIME-PUSHD/DELT*GDAY)
      EGDAY   = INTGRL(0.,PUSHD*TIME-PUSHD/DELT*EGDAY)
      DRAIN   = WIN(N+1)
      TDRAIN  = INTGRL(0.,DRAIN)
      TRAIN   = INTGRL(0.,RAIN)
```

```
      TOTINF  = INTGRL(0.,INFR)
      TEVAP   = INTGRL(0.,SEVAP)
      TOTRAN  = INTGRL(0.,STRAN)
      ET      = INTGRL(0.,SEVAP+STRAN)
      FUNCTION RAINTB = 0.,0.,4.,0.,5.,25.,6.,0.,9.,0.,10.,25.,...
                        11.,0.,14.,0.,15.,25.,16.,0.,19.,0.,20.,...
                        25.,21.,0.,24.,0.,25.,25.,26.,0.,29.,0.,...
                        30.,25.,31.,0.,34.,0.,35.,25.,36.,0.,39.,0.,...
                        40.,25.,41.,0.,44.,0.,45.,25.,46.,0.,49.,0.,...
                        50.,25.,51.,0.,54.,0.,55.,25.,56.,0.,59.,0.,.
                        60.,25.,61.,0.,64.,0.,65.,25.,66.,0.,69.,0.,.
                        70.,25.,71.,0.,74.,0.,75.,25.,76.,0.,79.,0.,.
                        80.,25.,81.,0.,84.,0.,85.,25.,86.,0.,89.,0.,.
                        90.,25.,91.,0.,94.,0.,95.,25.,96.,0.,99.,0.,.
                        100.,0.
*     FUNCTION EVPTB =  0.,4.,31.,4.,32.,5.,59.,5.,60.,6.,90.,6.,...
*                       91.,6.5,151.,6.5,152.,6.,212.,6.,213.,5.,...
*                       243.,5.,244.,5.5,304.,5.5,305.,4.5, 334.,4.5,.
*                       335.,4.,365.,4.
      FUNCTION PEINRT = 91.,6.3,105.,6.3,135.,7.0,166.,6.9,196.,6.1,...
                        227.,5.9,258.,5.8,288.,5.3,304.,5.3
      FUNCTION PETRT  = 91.,4.3,105.,4.3,135.,5.0,166.,4.9,196.,4.1,...
                        227.,3.9,258.,3.8,288.,3.3,304.,3.3
      FUNCTION ROFINT = 0.,0.,5.,0.2,10.,0.5,20.,1.2,30.,1.55,...
                        70.,1.7,200.,1.7
      FUNCTION EFFACT = -10.,0.,0.,0.,0.4,1.,1.1,1.
      FUNCTION SSWTB  = 0.,500.,250.,500.,400.,600.,15000.,600.
      FUNCTION MFT    = 0.,0.,.25,.05,.5,.3,.75,.75,1.,1.,1.5,.5
      TABLE FLDCAP(1-3) = 0.225, 0.145, 0.09
      TABLE WLTPNT(1-3) = 0.075, 0.055, 0.028
      TABLE AIRDRY(1-3) = 0.025, 0.018, 0.009
      TABLE BOUND(1-3)  = 150, 1200, 3001
      TABLE IAVW(1-23)  = 23*0.
      PARAM STDAY  = 0.
      PARAM ISOHC  = 1.
```

```
PARAM RNOFFC = 0.2
PARAM EVAPC  = 3.3
PARAM PROP   = 15., IMF    = 0.4
PARAM GERMT  = 1.5, GDPTH  = 50.
PARAM IBIOM  = 15., RGR = 0.15, DGRATE = 35., PDGRTM = 250.
PARAM RTDG   = 75., OGRTD = 40., MXRTD = 1500.
PARAM IFRNB  = 0.025, IFRMN = 0.013, NUE = 0.9, LE = 0.7
PARAM FRNLIT = 0.0075, FRNR = 0.0092, NCR = 0.0125
PARAM RDR    = 0.05, RDLIT = 0.05, ILIT = 500.
PARAM DEADT  = 4.
PARAM HRVST  = 300.
PRINT W(1-23),  TDRAIN,   TRAIN,    TOTINF,   TOTRAN,   TEVAP,   ...
      ET,       RTD,      TGROWD,   GDAY,     GERWAV,   GRRATE,  ...
      TDBIOM,   TNITUP,   NCBIOM,   NDBIOM,   TMINR,    TMINL,   ...
      TMINRL,   TSUBST,   TAVW,     TAVW1,    STRAN,    TRANP,   ...
      SEVAP,    AEVAP,    WTOTR,    LITTER,   BIOM,     WIN(1),  ...
      EVAPPR,   EVAPP
OUTPUT RGROW,TRR,BIOM,SCOV,NFACT
PAGE NTAB = 3, SYMBOL = (R,T,B,S,N)
OUTPUT TNITUP, NCBIOM,NDBIOM,TMINR,TMINRL
PAGE NTAB = 5, SYMBOL = (T, L, D, R, M)
TIMER FINTIM = 0., DELT = 1., PRDEL = 1., OUTDEL = 1.
METHOD RECT
END
```

Appendix 2. WBNLIM variable definitions.

AEVAP	Actual soil evaporation rate not considering daily rainfall-enhanced evaporation (mm/day)
AIRDR	Volumetric water content of a soil layer when air dry (m^3/m^3)
AIRDRY	Volumetric water content of a soil horizon when air dry (m^3/m^3)
AVW	Number of days water content of a soil layer is above wilting point (d)
AVW 1	AVW weighted by function relating rate of decomposition of organic material to soil moisture content (d)
BIOM	Weight of live shoot (kg DM/ha)
BOUND	Depth of boundary between soil horizons (mm)
CROPSI	Initial crop status (CROPST) (-)
CROPST	Crop status indicating live standing crop present (CROPST = 1) or not (CROPST = 0)
DAY	Number of days in the year from 1 January
DEADT	Duration of no transpiration before death (d)
DELT	Time step of calculations
DGRATE	Nutrient limited potential shoot growth rate (kg DM/ha/d)
DEPTH	Depth of top of a soil layer (mm)
DEPTHC	Depth of center of a soil layer (mm)
DRAIN	Water drained below the deepest soil layer (mm)
DSLER	Number of days plus 1 since last effective rain (d)
EFFAC	Reduction factor for root effectiveness as a function of soil moisture content (-)
EFFACT	Table of EFFAC versus reduced soil moisture content (-)
EGDAY	Day number of end of last growing period
EMPTR	Rate seed imbibition period is reduced when soil becomes too dry prior to germination (d/d)
EMPTRR	Rate drought period without transpiration is reduced when transpiration resumes (d/d)
ET	Cumulative sum of evapotranspiration (mm)

EVAPC	Experimentally determined evaporation constant (mm/d)
EVAPP	Soil evaporation rate potential (mm/d)
EVAPR	Actual evaporation rate from a soil layer (mm/d)
EVAPTR	Potential evapotranspiration rate (mm/d)
EVPTB	Table of Penman potential evaporation rates (mm/d)
F	Normalized fraction of soil evaporation from a soil layer (-)
FINTIM	Last simulation day number
FLDCAP	Volumetric water content of a soil horizon at field capacity (m^3/m^3)
FLDCP	Volumetric water content of a soil layer at field capacity (m^3/m^3)
FRNLIT	Fraction of nitrogen in litter (-)
FRNR	Fraction of nitrogen in dead root organic matter (-)
GDAY	Last germination day number
GDPTH	Seed depth (mm)
GERD	Indicator that seeds are being wetted (GERD = 0) or not (GERD = 1) (-)
GERMT	Number of days seeds need to be wetted before germination (d)
GERWAV	Germination wave number
GROWD	Indicator that the day is a growth day (GROWD = 1) or not (GROWD = 0)
GRRATE	Shoot growth rate (kg DM/ha/d)
GRTD	Root extension rate (mm/d)
IAVW	Initial available water index (AVW) (d)
IBIOM	Initial weight of shoots (BIOM) (kg DM/ha)
IFRMN	Initial fraction of nitrogen mineralised from dead root organic matter (-)
IFRNB	Fraction of nitrogen in IBIOM (-)
ILIT	Initial weight of litter (kg DM/ha)
INFR	Soil water infiltration rate (mm/d)
INI	Initial mineralised nitrogen in a soil layer (kg/ha)
INTC	Rainfall interception rate by litter and plants (mm/d)
ISOHC	Isohyet correction factor (-)
K	Soil horizon number

KILD	Indicator of transpiration (KILD = 1) or not (KILD = 0) (-)
LE	Leaching efficiency factor (-)
LITTER	Weight of litter (kg DM/ha)
LMF	Threshold fraction of available water below which reduced transpiration occurs (-)
MF	Moisture factor relating rate of decomposition of organic material to moisture content of a soil layer (-)
MFT	Function relating rate of decomposition of organic material to soil moisture content (-)
MSFD	Rate of increase in drought period without transpiration prior to death (d/d)
MSFG	Rate of increase in seed imbibition period for germination (d/d)
MSSTAT	Soil moisture status (if positive then water in root zone is above wilting point)
MSSTD	Duration of drought period without transpiration (d)
MSSTG	Duration of seed imbibition for germination (d)
MXRTD	Maximum rooting depth (mm)
N	Number of soil layers simulated
NCBIOM	Nitrogen concentration in shoot (kg N/kg DM)
NCONC	Mineralised nitrogen concentration in water in a soil layer (kg N/mm)
NCR	Nitrogen concentration in rainfall and associated biological nitrogen fixation (bacteria, algae, up to 5% ambient legumes in shoots) (kg/mm)
NDBIOM	Nitrogen concentration in dead shoots (kg N/kg DM)
NFACT	Reduction factor on potential transpiration due to nutrient limitation (-)
NI	Mineralised nitrogen in a soil layer (kg N/ha)
NLEACH	Rate of nitrogen leached from a soil layer (kg N/ha/d)
NUE	Nitrogen uptake efficiency factor (-)
NUPTAK	Rate of nitrogen uptake into shoots from a soil layer (kg N/ha/d)
OGRTD	Potential root growth rate (mm/d)
PDGRT	Potential shoot growth rate (kg DM/ha/d)

PDGRIM	Maximum potential shoot growth rate (kg DM/ha/d)
PROP	Extinction factor for soil moisture withdrawal (-)
PUSHD	Indicator of crop death (PUSHD = 1) or not (PUSHD = 0) (-)
PUSHE	Indicator of germination (PUSHE = 1) or not (PUSHE = 0) (-)
RAIN	Rainfall (mm/d)
RAINTB	Rainfall table (mm/d)
RAVW	Rate of increase in AVW (d/d)
RAVW1	Rate of increase in AVW1 (d/d)
RCLIT	Litter decomposition rate (kg DM/ha/d)
RCN	Rate of change of mineralised nitrogen in a soil layer (kg N/ha/d)
RCSUBS	Rate of dead root organic matter decomposition in a soil layer, negatively signed (kg DM/ha/d)
RCW	Rate of change in water content for a soil layer (mm/d)
RDENF	Normalised root density factor for a soil layer (-)
RDLIT	Relative decomposition rate of litter (/d)
RDR	Relative decomposition rate of dead root organic matter (/d)
RDSUBS	Rate of dead root organic matter decomposition in a soil layer, negatively signed (kg Dm/ha/d)
REDF	Reduction factor for water uptake (-)
RGR	Relative growth rate of shoots (/d)
RGROW	Actual water-or nutrient-limited growth rate (/d)
RNMIN	Rate of nitrogen mineralisation from dead root organic matter in a soil layer (kg N/ha/d)
RNMLIT	Rate of nitrogen mineralisation from litter (kg N/ha/d)
RNOFF	Rate of runoff (mm/d)
RNOFFC	Average long-term fraction of annual rainfall that runs off (-)
RNPAR	Rainfall parity (0 or 1 on rainfree and rainy days, respectively)
ROFINT	Fraction relating fraction of average long-term runoff to individual storm size (-)
RRDENF	Relative root density factor (-)
RTD	Rooting depth (mm)
RTDG	Initial rooting depth after germination (mm)

RTDI	Initial rooting depth (mm)
SCOV	Fraction of soil covered by shoot (-)
SEVAP	Actual soil evaporation rate (mm/d)
SSWTB	Specific shoot weight table (kg DM/ha)
STDAY	Starting day of simulation
STORC	Volumetric available water storage capacity of a soil layer (m^3/m^3)
STRAN	Actual transpiration rate (mm/d)
SUBSTI	Initial weight of dead root organic matter in a soil layer (kg DM/ha)
SUBSTR	Weight dead root organic matter in a soil layer (kg DM/ha)
SUMRRD	Sum of relative root density factors (-)
SUMT	Soil layer thickness weighted sum of VAR factors (mm)
SWPDS	Indicator if soil layer containing root tip is above wilting point (SWPDS = 1) or not (SWPDS = 0)
TAVW	Cumulative sum of AVW (d)
TAVW1	Cumulative sum of AVW1 (d)
TCK	Thickness of a soil layer (mm)
TDBIOM	Weight of dead shoot (kg DM/ha)
TDEPTH	Depth of soil simulated (mm)
TDRAIN	Cumulative sum of water drained below the deepest simulated soil layer (mm)
TEVAP	Cumulative sum of soil evaporation (mm)
TGROWD	Cumulative sum of number of growing days (d)
TIME	Simulated time
TMINL	Cumulative sum of nitrogen mineralised from litter (kg N/ha)
TMINR	Cumulative sum of nitrogen mineralised from dead root organic matter (kg N/ha)
TMINRL	Cumulative sum of nitrogen mineralised from litter and dead root organic matter (kg N/ha)
TNITUP	Cumulative sum of nitrogen taken up in shoots (kg N/ha)
TOTINF	Cumulative sum of infiltrated water (mm)
TOTNI	Mineralised nitrogen in the soil (kg N/ha)

TOTNUP	Rate of nitrogen taken up in shoots (kg N/ha/d)
TOTRAN	Cumulative sum of transpiration (mm)
TRAIN	Cumulative sum of rainfall (mm)
TRAN	Actual transpiration rate from a soil layer (mm/d)
TRANP	Potential transpiration rate (mm/d)
TRNMIN	Rate of nitrogen mineralisation from dead root organic matter (kg N/ha/d)
TRR	Ratio of actual to potential transpiration (-)
TSUBST	Weight of dead root organic matter in the soil (kg DM/ha)
VAR	Soil water content weighted extinction (with depth) factor (-)
W	Water content of a soil layer (mm)
WGER	Water content of a soil layer containing seed and any other layers above the seed (mm)
WI	Initial soil water content of a soil layer (mm)
WIN	Flux of water into a soil layer (mm)
WLTPNT	Volumetric water content of a soil horizon at wilting point (m^3/m^3)
WLTPT	Volumetric water content of a soil layer at wilting point (m^3/m^3)
WTOTR	Water content within the root zone (mm)

Discussion

Question - How does Figure 3, showing higher nitrogen uptake with longer wetting, match with the remark that the more water in a non-fertilized situation, the lower the quality?

Answer - Figure 3 shows that higher rainfall or rather deeper wetting and longer duration of wetting, which are not only a function of the amount of rain but also of its distribution, increases the availability of nitrogen. But it increases dry-matter production more, so that the nitrogen concentration in the material is lower. In a situation where growth is nitrogen-limited, the nitrogen is always diluted to its minimum value, which is not the case where growth is water-limited.

Question - In the model does the amount of available N depend on the amount of biomass from the previous season or is it the amount of N that was in the system last year?

Answer - It is the total amount of nitrogen in the organic material produced last year, i.e. it is assumed that the stable component in the organic material has very little influence on the total nitrogen uptake. The year after a drought year is partly compensated by the fact that the plants in a dry year have not been able to take up all the available nitrogen. There is a carry-over of mineral nitrogen, as has also been shown in Migda (Israel).

Question - Do you assume a constant seed stock?

Answer - No, for each site the biomass at the end of germination is estimated on the basis of specific knowledge about the site, such as seedstock and germination characteristics of the soil type.

Question - The suggestion of a positive correlation between soil wetness and N availability seems contradictory to the information that after the first rain the microbial population increases all of a sudden leading to nitrogen immobilisation followed only later, when those microbes die, by release.

Answer - The discussion about the existence or non-existence of the nitrogen flush is continuing. Experimental work by Birch and others in East Africa suggested a flush of mineral nitrogen after the first rain. The phenomenon was explained by the fact that in the summer, part of the microbial population died. When the soil is rewetted, it forms the substrate for decomposition with a low ratio of carbon to nitrogen, providing the nitrogen flush. The results from work in West Africa point more in the direction of a relationship between total rainfall and accumulated mineral nitrogen.

Statement - A similar problem in the water balance model, as described in the paper, was observed when a model developed in India was applied elsewhere.

Answer - The point is that total evapotranspiration is fairly well predicted as is infiltration. Hence the problem is a completely different distribution in the soil. Such large discrepancies between predicted distribution and that actually measured have never occurred before.

Question - How do you explain the direct relationship between moisture availability and nitrogen concentration? If it is an annual pasture, is there not going to be a change in pasture species towards those which are able to complete their growth and maturation?

Answer - One should distinguish between two processes: the plant can mature and set seed and complete its phenological development but it cannot dilute the nitrogen that it has taken up.

Under conditions where nitrogen is not too limiting the relationship between yield and total nitrogen in vegetation at about flowering will have a slope of about 2 kg N/kg DM. In a situation where water is limiting, dry matter will increase by only a limited amount after flowering. At maturity the concentration will then be 0.015 kg N/kg DM. In a good year on the other hand, dry-matter production after flowering may be substantial and the end result will be a concentration of say 0.0075 kg N/kg DM. It is a matter of how much additional structural material the plant can produce. Thus the variability in dry-matter production as a function of moisture availability is much greater than that in total uptake of nitrogen, and therefore the quality changes from year to year and from site to site.

Question - Are the experimental results based on analysis of the same tissue of the same plant species in different years?

Answer - Yes, that is the case.

Question - Does the nitrogen concentration in the seeds vary?

Answer - The nitrogen concentration in the seed can vary. When growth is nitrogen-limited the concentration may be around 1%, under water-limited conditions much higher. The same phenomenon occurs in wheat grains, which in a dry year may contain 20% protein. The concentration of nitrogen in the seed is usually high shortly after seed set and the nitrogen is diluted with carbohydrates coming into the seed. The rate at which the nitrogen concentration decreases depends on the rate of influx of both carbohydrates and nitrogen coming from tissues that are being depleted. Some plants stay green and hold on to the nitrogen for a long time, so the nitrogen concentration falls sharply; other plants tend to ripen rapidly and lose the nitrogen more quickly and the dilution proceeds more slowly. The final concentration depends on where the dilution process stops.